

GENETICS OF LUPINUS. III. EVIDENCE FOR GENETIC DIFFERENTIATION AND COLONIZATION IN LUPINUS SUCCULENTUS (FABACEAE)

JAMES HARDING and C. B. MANKINEN

Department of Environmental Horticulture, University
of California, Davis 95616

Many species of higher plants occupy a diversity of habitats which results in the formation of localized races or ecotypes. The concept that genetic differentiation exists among natural populations of a species is well established and it is no longer necessary to review the evidence. It is clearly not enough to acknowledge that variation exists. It is necessary to understand the ecological factors which have contributed to genetic differentiation between populations. Why is a gene in high frequency in one population and in lower frequency or absent in another population? It is equally important to understand the genetic differences in greater detail. For example, are differences between populations the result of fixed-gene differences, gene frequency differences, or chromosomal differences? In cases where evidence is available on genetic differences (e.g., Epling, Lewis and Ball, 1960; Jain and Joshi, 1962; Weil and Allard, 1965) evidence on ecological differences is lacking. Where ecological evidence is available (e.g., Bradshaw, 1959; 1960) genetic differences are not understood. Both genetic and ecological differences have been studied in *Ricinus communis* (Harland, 1947) and *Trifolium repens* (Daday, 1958). In these cases the resulting genetic structure could be related to ecological variables.

Comparative studies of colonizing and non-colonizing species have also received the attention of geneticists and ecologists. Genetic variability has been studied in the following, recently introduced, species: *Bromus mollis* (Knowles, 1943), *Ricinus communis* (Harland, 1947), *Trifolium subterraneum* (Morley, 1958), *Avena fatua* (Imam and Allard, 1965), and *Avena fatua* and *A. barbata* (Jain and Marshall, 1967). The results of these investigations can be compared to those obtained from investigations of the following, relatively non-colonizing species: *Linanthus parryae* (Epling and Dobzhansky, 1942), *Collinsia heterophylla* (Weil and Allard, 1965) and *Festuca microstachys* (Kannenbergh and Allard, 1967). Comparisons between colonizing and non-colonizing species are discussed throughout the symposium *The Genetics of Colonizing Species*. In that symposium Lewontin (1965) suggests that emphasis should be placed on colonizing episodes rather than on the a posteriori study of colonizing species. Harper (1965) advises the creation of colonizing episodes by experimental introduction and states that such experiments may "reveal quite simple and fundamental properties of plant populations which classical descriptive ecology cannot uncover."

The introduction of founders into a new habitat does not always result in successful colonization, as shown by Sagar and Harper (1960). The advantages offered by California natives, which have become weedy (colonizing) since the agricultural revolution so drastically changed the ecology of the Central Valley of California, have been pointed out by Stebbins (1965). These species can be studied in their natural (original) habitats as well as in agricultural habitats where they have become colonizing agrestals. Colonizing episodes can be followed from their inceptions by both geneticists and ecologists.

Another possibility is the study of natural populations and their descendant roadside (ruderal) populations which are abundant throughout the foothills and mountains of California. *Lupinus succulentus* Dougl. is an annual California native which has become ruderal in many areas (Stebbins, 1965). There are now many more roadside populations than natural populations. Natural populations tend to occur in habitats with a considerable degree of disturbance suggesting that this species may have been preadapted for colonization. Since road-building is continuing, colonizing episodes are constantly initiated. In some cases, founders can be traced to their parental natural population. Some populations may be available for long-term studies, but many are transient and available for only a few years. Nevertheless, such populations offer unique opportunities for both ecological and genetical studies on population differentiation during the early stages of colonization.

The paper reports the results of an investigation concerning four loci in *L. succulentus*. Surveys of genotypic frequencies in natural and ruderal populations were made over a large geographic area and genetic polymorphism is related to seasonal fluctuations and to differences in the degree of disturbance of the habitat.

GENETICS

The papilionaceous flowers of *L. succulentus* are predominantly dark blue except for the white sulcus of the banner. Rarely, there occurs an entirely white flowered variant. Crosses between wild-type (blue) and white gave an F_2 segregation ratio of 53:24, wildtype: white. Pink flowered plants occur rarely and when crossed to wild-type gave an F_2 ratio of 81:27, wild-type: pink. These results are in accord with the inheritance of white and pink in *Lupinus nanus* Dougl. (Harding and Mankinen, 1967) and analogous genetic symbols will be assigned, viz. bb for white and pp for pink. Light blue flowered plants are observed more frequently and crosses to wild-type gave an F_2 ratio of 89:26, wild-type: light blue (designated dd). The presence or absence of a band of dark pigmentation across the seed coat was found to segregate 85:30, band: no band. The recessive, lacking the band, is designated ss. Chi-square tests indicate that none of these ratios depart significantly from the 3:1 Mendelian expectation.



FIG. 1. Northern half of California showing collection areas A through G.

Since some populations are polymorphic for D/d and S/s, the linkage relationship is of interest. The F_2 coupling phase dihybrid ratio was 85:4:0:26 for D-S-:D-ss-ddS-:ddss, which deviates significantly from the expected 9:3:3:1. The maximum likelihood estimate of the recombination fraction, r , is given by the solution of

$$85 \frac{2r - 2}{r^2 - 2r + 3} + 4 \frac{2r - 2}{r^2 - 2r} + 26 \frac{2}{r - 1} = 0.$$

Use of Allard's tables (Allard, 1956) results in an estimate of $r = .04$ with a standard error of .02. Thus, D/d and S/s are very closely linked.

GEOGRAPHIC VARIATION

The distribution of *L. succulentus* is disjunct with the largest concentration along the Pacific Coast of California. This coastal group is represented by many populations from Mendocino County, California,



FIG. 2. Southern half of California showing collection areas G through P. Note some overlap with FIG. 1.

to northernmost Baja California, Mexico (Munz, 1959). These populations occur in the foothills of the North Coast, South Coast, Transverse, and Peninsular Ranges and on the off shore islands of San Clemente (Raven, 1963), Santa Catalina (Thorne, 1967), Anacapa, San Miguel, Santa Cruz and Santa Rosa (Philbrick and Emery, pers. comm.). The interior group occurs in the Pinal and Mazatzal Mountains (Gila and Maricopa counties) of Arizona (Kearney and Peebles, 1951). Since differences are not yet understood, the loose terms coastal taxon and interior taxon will be used to avoid questions regarding possible sub-specific epithets.

The present study is based on the coastal group, including populations from the North and South Coast Ranges, the Transverse and Peninsular Ranges, and the Central Valley. Collection areas are given

by the letters A through F in Fig. 1 and by the letters G through P in Fig. 2. Area A includes the north end of the Sacramento Valley. The Red Bluff, Tehema, Corning, and Orland populations are ruderals along Interstate Highway 5 and varied in size from 300 to 1000 plants in 1968. Area B is northwest of Lake Berryessa between Putah Creek and Pope Creek. The upper Putah populations lie between Pope Creek and Pope Canyon Road on highly eroded slopes. Population size ranged from 300 to more than 30,000 plants in 1967. Area C includes Putah Canyon from Monticello Dam to the valley floor and the foothills between Putah Canyon and Cache Canyon. The Lower Putah populations are situated serially along Highway 128 and are ruderal with varying degrees of disturbance. They vary in size from 200 to approximately 1,500 plants in most years studied. The Mace populations are located near Cottonwood Creek and appear to be relatively undisturbed, except for natural erosion. Mace-30 was approximately 1000 plants in 1967 and Mace-11 became extinct after a population size of 100 was observed in 1963. The valley floor in the vicinity of Davis is designated Area D. Most populations on the valley floor are small, ephemeral colonies. The El Macero populations, which were located along the Southern Pacific railway between Davis and Sacramento, are now extinct. The Davis-1 population is located on a road cut along Interstate Highway 80 on the west edge of Davis and was composed of 328 plants in 1968. Area E includes the foothills in the vicinity of Vacaville and Vallejo. The Vacaville populations are large and occur along the north side of Interstate Highway 80 between Vacaville and Fairfield with varying degrees of disturbance.

In the South Coast Ranges Area F includes the coastal fog-belt along the Pacific Ocean between San Francisco and Santa Cruz. The San Gregorio population is located in the San Gregorio Beach State Park on a steep slope immediately adjoining the beach within reach of the spray and included approximately 80 plants in 1967. The dry foothills of the South Coast Ranges from Coalinga to Taft are designated Area G. The Tar Canyon population is large and is located southwest of Avenal with relatively little signs of disturbance. The Reef City-1 population is ruderal along State Highway 41 between Reef City and Cholame. It included 50 to 60 plants in 1968. Area H includes the coastal area from Atascadero to Santa Maria. The San Luis Obispo-1 population is a roadside colony along U. S. Highway 101, approximately six miles south of San Luis Obispo and was composed of approximately 500 plants in 1968.

In the Transverse Ranges, Area J includes the north-western half of the Santa Ynez Mountains and River Valley. The Lompoc populations are ruderal along State Highway 1 between Lompoc and Las Cruces. They varied in size from approximately 50 to 300 individuals in 1968. The Solvang-1 population was a very small colony of approximately

TABLE 1. FREQUENCIES AND BINOMIAL STANDARD ERRORS FOR DOMINANTS AT THE S/s and D/d LOCI FROM 1962, 1963, 1966 AND 1967 COLLECTIONS. THESE POPULATIONS WERE MONOMORPHIC BBPP.

POPULATION		YEAR	FREQUENCY		
			S-	D-	
AREA B					
Upper Putah	— 1	1967	.26 ± .036	Mono DD	
	— 2	1967	.10 ± .025	Mono DD	
	— 3	1967	.41 ± .042	Mono DD	
	— 4	1967	.70 ± .019	Mono DD	
AREA D					
El Macero	— 1	1962	.05 ± .026	Mono DD	
	— 3	1962	.02 ± .016	Mono DD	
AREA E					
Vacaville	— 1	1963	.33 ± .023	Mono DD	
	— 2	1963	.03 ± .016	Mono DD	
AREA F					
San Gregorio	— 1	1967	Mono ss	Mono DD	
AREA G					
Tar Canyon	— 2	1967	.81 ± .038	Mono DD	
AREA C					
Lower Putah	— 1	1962	.38 ± .069	Poly D/d	
	— 2	1962	.46 ± .094	Poly D/d	
	— 1	1963	.76 ± .051	.03 ± .025	
	— 2	1963	.36 ± .063	.40 ± .036	
	— 2	1966	.42 ± .047	.49 ± .058	
	— 3	1966	.14 ± .035	.95 ± .022	
	— 4	1966	.14 ± .031	.87 ± .030	
	— 5	1966	.10 ± .028	.95 ± .021	
	— 2	1967	.42 ± .046	.30 ± .040	
	— 3	1967	.18 ± .039	.95 ± .026	
	— 4	1967	.14 ± .034	.91 ± .025	
	— 5	1967	.14 ± .026	.94 ± .013	
	Mace	— 11	1962	Mono ss	Mono DD
		— 30	1967	.01 ± .008	Mono DD

40 plants in 1968, occurring near State Highway 246 on a highly disturbed site. Area K is the south-eastern half of the Santa Ynez Range and includes the Santa Barbara populations which ranged in size from approximately 100 to 150 plants in 1968. These roadside colonies occur along State Highway 154 between Santa Barbara and San Marcos Pass. Area L includes the interior Ranges between Newhall and the Tejon Pass. The Castaic populations are large ruderals varying in size from approximately 300 to 2000 individuals in 1968, and are situated along Interstate Highway 5 approximately three miles north of Castaic.

In the Peninsular Ranges, Area M includes the area from Lake Elsinore to Fallbrook. The Murrieta population, approximately 200 plants in 1968, occurs along State Highway 71 just east of Murrieta. Area N includes the coastal strip between Del Mar and San Clemente. The Vista-1 population, with approximately 500 plants in 1968, occurs on a recent road fill along State Highway 78 south of Vista. The southern-

TABLE 2. FREQUENCIES AND BINOMINAL STANDARD ERRORS FOR S/s LOCUS FROM 1968 COLLECTIONS.

Population	Frequency S-	Population	Frequency S-
AREA A		AREA D	
Red Bluff — 1	.47 \pm .043	Davis — 1	.03 \pm .019
Tehema — 1	.79 \pm .035	AREA K	
Corning — 1	.13 \pm .031	Santa Barbara — 1	.62 \pm .056
Orland — 1	.77 \pm .037	— 2	.70 \pm .069
— 2	.77 \pm .062	AREA L	
AREA G		Castaic — 1	.36 \pm .055
Reef City — 1	.17 \pm .059	— 2	.70 \pm .044
AREA H		AREA M	
San Luis Obispo — 1	.27 \pm .036	Murrieta — 1	.52 \pm .096
AREA J		AREA N	
Lompoc — 1	.85 \pm .068	Vista — 1	.32 \pm .039
— 2	.46 \pm .040	AREA P	
Solvang — 1	.71 \pm .099	Mission Bay — 1	Mono ss

most populations, including the San Diego and Tijuana areas are designated Area P. This includes the highly disturbed Mission Bay population which had approximately 100 plants in 1968.

The results indicate that all populations sampled are monomorphic BBPP. There were three questionable exceptions: the B/b locus in a small colony in Cowell Valley (Area C), the occurrence of three bb in Davis-1 (Area D), and the P/p locus in a small colony near Winters (Area D). The D/d locus is monomorphic DD in all populations sampled except the Lower Putah Populations (table 1) which have varying frequencies of dd. The relatively infrequent occurrence of polymorphisms for loci affecting flower color may result from natural selection favoring the dark blue color through pollinator preference. In contrast, the S/s locus is polymorphic in nearly all populations sampled (tables 1 and 2). The only exceptions are Mace-11, San Gregorio-1 (based on only 34 individuals, i.e. 68 s alleles) and Mission Bay-1. Populations, therefore, are generally homozygous BBPPDD and polymorphic for the alleles S and s. The Lower Putah Populations are notable exceptions, being polymorphic for D and d. The Lower Putah populations were sampled because they were polymorphic for D/d but seed coat variation for S/s was not observed until after the selection of populations to be sampled was made. Consequently, the populations studied are a random sample of *L. succulentus* populations with respect to the S/s locus and the observed ubiquity of this polymorphism is not biased by the choice of populations.

CLINAL AND SEASONAL VARIATION

When the Lower Putah populations were first observed in 1960, it appeared that the frequency of dd was low at the base of the canyon

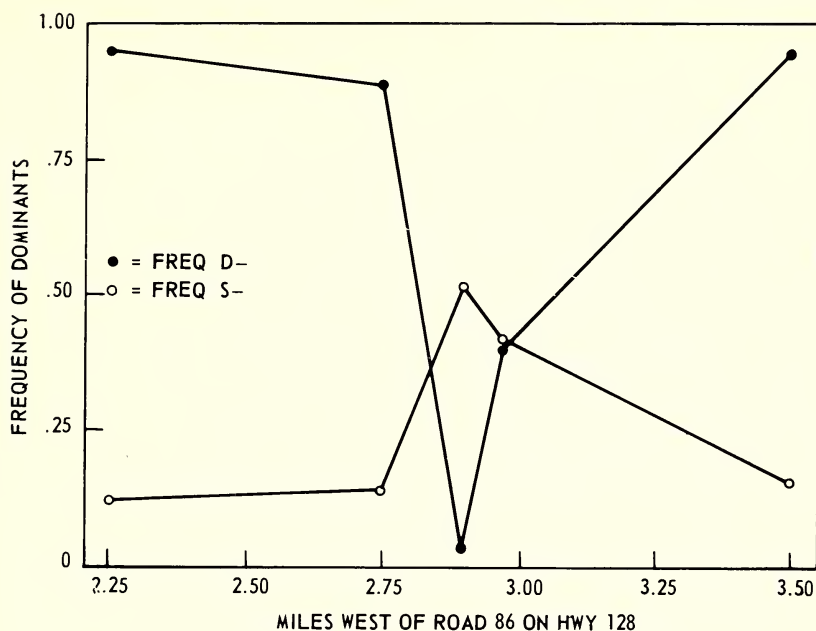


FIG. 3. Frequency of D- and S- in Lower Putah Canyon populations, plotted against distance in miles from an arbitrary point near the mouth of the canyon.

and increased in frequency as the canyon was ascended. After reaching a frequency of more than 50 per cent, the frequency of dd was quickly reduced in subsequent populations near the head of the canyon. The five Lower Putah populations were selected at more or less equally spaced intervals. The frequencies, plotted in Fig. 3, represent means for each population taken over the years sampled (table 1). The miles are measured from a purely arbitrary intersection of roads. Figure 3 shows the predominance of D-ss at both ends of the area with sharp increases of dd and S- in a segment less than one-half mile in length. This represents a sharp increase in genetic variability for D/d and S/s over a very short distance. These distances are well within the radius of activity of the predominant pollinating agent *Apis mellifera* L. The inter-relationship between the linked D/d and S/s loci will be the subject of another paper in this series.

Over the period of 8 years the frequencies in Putah Canyon populations appeared fairly stable. Those populations which have been sampled in more than one year are summarized in Fig. 4. The populations could not be sampled in 1964 and 1968 because there were very few plants presumably due to very low rainfall in those years. Their immediate return to large numbers in 1965 suggests that many seeds remain hard and overwinter during years of low winter rainfall.

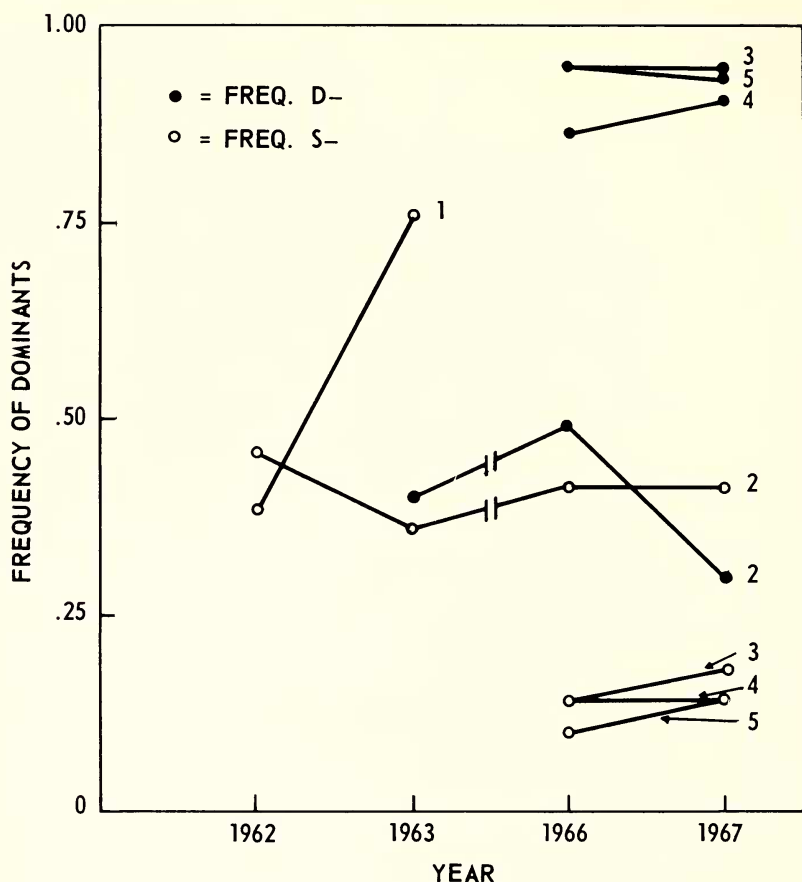


FIG. 4. Frequency of D- and S- in Lower Putah Canyon populations for the years sampled 1964, 1965 and 1968 were not sampled (see text).

Considering the seasonal fluctuations in gene frequency which may be expected in plant populations (e.g. Allard and Workman, 1963) the fluctuations are not great with the exception of S/s in Lower Putah-1 in 1962 and 1963. This population occurred on such a highly disturbed slope that it was abandoned after 1963. Although the remaining four populations are not likely in gene frequency equilibrium, they show a fair degree of stability considering their ruderal nature.

INTRA-POPULATION DIFFERENTIATION

The Vacaville-1 population occupied a very large road-cut, 116 feet across, with population size more than 3,000 individuals in 1963. For convenience of collection the population was arbitrarily subdivided into four sub-populations according to the schematic representation in

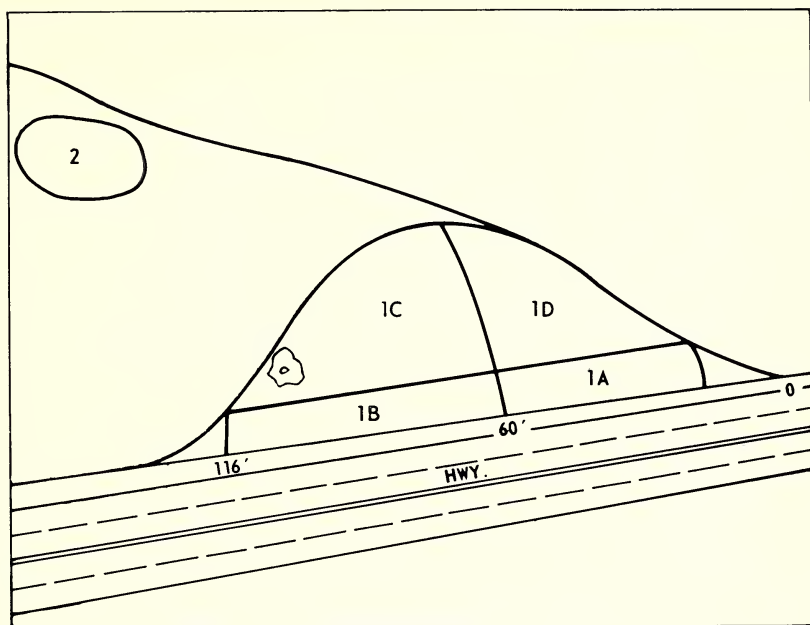


FIG. 5. Schematic representation of the sub-division of Vacaville -1 and -2 in 1963. The highway was U. S. Highway 40, now Interstate 80.

Fig. 5. Although the frequency of S- in the population as a whole was .33, the frequencies in the sub-populations were: 1C-: $.47 \pm .047$; 1D-: $.18 \pm .039$; 1B-: $.50 \pm .050$; and 1A-: $.17 \pm .036$. The frequencies and standard errors clearly indicate that 1A and 1D can be taken as one group and 1B and 1C as another group. Topographically, the difference is between the two sides of the population. However, further vertical subdivision might have revealed a continuous gradation across the population, i.e., an intrapopulation cline or microcline. This possibility could not be investigated because the population was subsequently destroyed by highway construction.

Another large population, Upper Putah-4, was chosen for further studies on intra-population differentiation. This population occupies a large highly disturbed hillside of approximately two acres with considerable variation in topography and population density. Population size was approximated at more than 30,000 and is probably nearer 50,000. It was subdivided and, although the subdivisions were based on gulleys and density gradients, they are considered fairly arbitrary because the population approaches one large continuum. The frequency of S- in the population was .70 and the frequencies in the sub-populations were: 4A-: $.79 \pm .033$; 4B-: $.75 \pm .034$; 4C-: $.74 \pm .035$; and 4D-: $.53 \pm .040$. The three sub-populations, 4A, 4B and 4C, are not significantly different, but sub-population 4D differs significantly from the rest. The

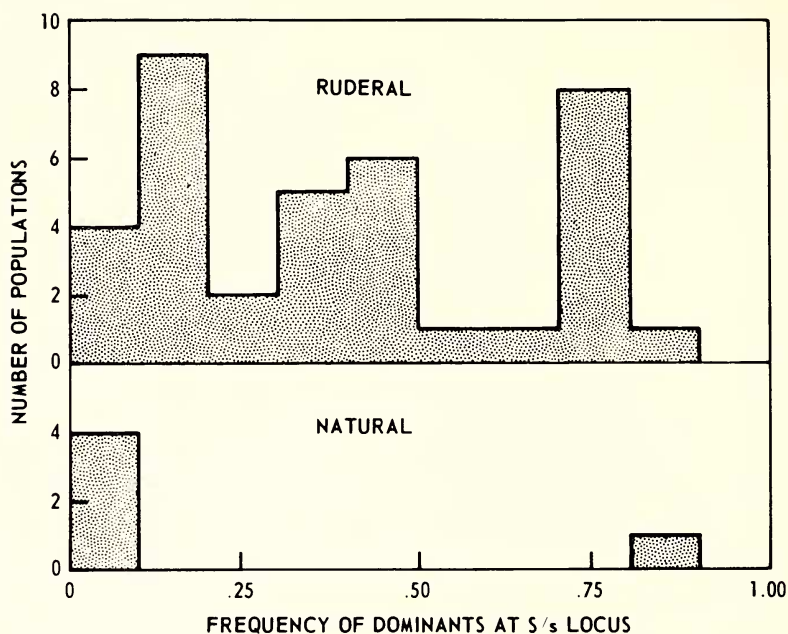


FIG. 6. Frequency of S- in all populations sampled, divided into those appearing natural and those ruderals appearing to be recently colonized.

frequency of S- is high in all sub-populations compared to the frequencies from other populations within Geographic Area-B, viz. .26, .10 and .41 (see table 1).

Population differentiation was not observed in all cases. Three subdivisions of Lower Putah-5 gave frequency estimates of .10, .13, and .16 for S-. The four subdivisions of Mace-30 gave estimates of 0, 0, .02 and .04. Two subdivisions of Castaic-2 gave estimates of .72 and .69 for S-. From these samples the extent of population differentiation cannot be determined. However, intrapopulational differences for the S/s locus were found in two of five populations studied.

COLONIZATION

The populations under study all occupy habitats with varying degrees of disturbance. Attempts were made to locate populations in habitats with a minimum of disturbance. The populations with the least apparent disturbance were the Mace populations, Vacaville-2, San Gregorio and Tar Canyon. The remaining populations are ruderals which probably colonized recently. This classification of populations as to relatively disturbed vs. relatively undisturbed is necessarily subjective and based on limited numbers of observations. The differences (fig. 6) suggest, however, that polymorphisms at the S/s locus are more frequent in more disturbed roadside habitats. Furthermore, the D/d poly-

morphisms and the possible B/b and P/p polymorphisms were found only in disturbed sites and these are not included in Fig. 6.

As a new colony is founded by a limited number of immigrants, genetic drift is expected to reduce the genetic variance to an extent inversely proportional to the number of founders and subsequent effective population size. To the contrary, genetic variance appears to have increased with colonization for the cases studied herein. This increased genetic variation in recently colonized populations may result from several causes. First, as new environments are encountered, new selective forces may also be encountered. For alleles at any particular locus this could result in a change in the direction of selection. In addition, the more disturbed habitats may exhibit more environmental variation leading to increased intrapopulation differentiation. Additional factors may include density dependent and frequency dependent selection.

In the case of the Vacaville populations it appears that Vacaville-1, on a highly disturbed cut, was founded by immigrants from Vacaville-2 (fig. 5). The road cut is deep into relatively undecomposed parent material, presumably low in nitrogen. The nitrogen fixing legume, *L. succulentus*, was apparently suited to colonize such an environment relatively free from the competition of grasses, at least in the early stages of colonization. With the colonization of Vacaville-1 the frequency of S- increased. If this were a purely random process, the majority of ruderal populations would be ss with an occasional population predominantly S-. But, as this is not the case, it appears that selection must have been involved. These hypotheses need testing in situ during the early stages of colonizing episodes and such episodes are presently being sought.

Baker (1965) discussed the various attributes which enable an annual to become a successful colonizer and concluded that "Probably no existing plant has them all." This appears to be the case for *L. succulentus*. While it is self-compatible, many pollen collecting insects cannot manipulate the large and specialized papilionaceous flower. This, however, could be compensated by the wide occurrence of *Apis mellifera*. *L. succulentus* has a tremendous seed fertility compared to most other species of *Lupinus* and dispenses its seeds by explosive dehiscence of the pods. Apparently, the colonizing characteristics of *L. succulentus*, particularly self-compatibility, fertility and dispersal, are sufficient to account for its recent success in colonization.

SUMMARY

Preliminary surveys indicate that most populations of *Lupinus succulentus* are genetically monomorphic for three flower color loci, viz., BB PP DD. In one small geographic area, a number of populations were polymorphic for the D/d locus. In this case, clinal variation and seasonal variation were found. The S/s locus which affects seed coat pigmenta-

tion was polymorphic in a large majority of populations and some genetic variation at this locus may be present in all but a very few colonies. Gene frequencies tended toward the limits of zero or one in populations from relatively undisturbed sites but tended toward one-half in the more disturbed ruderal populations presumed to be recently colonized. Five large populations were subdivided and genetic differentiation was found within two of these populations. No ecological basis has been found to account for population differentiation or for changes which occur during colonization. Various characteristics of *Lupinus succulentus*, in particular the dispersal of seeds and the high seed fertility, appear to be most important in determining its success in colonization.

ACKNOWLEDGMENTS

The authors thank R. W. Allard, D. G. Smeltzer, D. W. Kyhos, D. A. Watson, R. P. James, M. L. Schroeder, D. P. Drewes, and A. Horovitz for their suggestions and assistance and A. D. Mace for the privilege of working on his property.

This work is supported in part by NIH Grant GM 10476.

LITERATURE CITED

- ALLARD, R. W. 1956. Formulas and tables to facilitate the calculation of recombination values in heredity. *Hilgardia* 24:235-278.
- , and P. W. WORKMAN. 1963. Population studies in predominantly self-pollinated species. IV. Seasonal fluctuations in estimated values of genetic parameters in lima bean populations. *Evolution* 17:470-480.
- BAKER, H. G. 1965. Characteristics and modes of origin of weeds. In H. G. BAKER and G. L. STEBBINS (eds.), *The genetics of colonizing species*. Academic Press, New York.
- BRADSHAW, A. D. 1959. Population differentiation in *Agrostis tenuis* Sibth. I. Morphological differences. *New Phytol.* 59:92-103.
- DADAY, H. 1958. Gene frequencies in wild populations of *Trifolium repens*. III. World distribution. *Heredity* 12:169-184.
- EPLING, C., and T. DOBZHANSKY. 1942. Genetics of natural populations. VI. Microgeographical races in *Linanthus parryae*. *Genetics* 27:317-332.
- EPLING, C., H. LEWIS, and F. M. BALL. 1960. The breeding group and seed storage: a study in population dynamics. *Evolution* 14:238-255.
- HARDING, J., and C. B. MANKINEN. 1967. Genetics of *Lupinus*. I. Variations in flower color from natural populations of *Lupinus nanus*. *Canad. J. Bot.* 45: 1831-1836.
- HARLAND, S. C. 1947. An alteration in gene frequency in *Ricinus communis* L. due to climatic conditions. *Heredity* 1:120-125.
- HARPER, J. L. 1965. Establishment, aggression, and cohabitation in weedy species. In H. G. BAKER and G. L. STEBBINS (eds.), *The genetics of colonizing species*. Academic Press, New York.
- IMAM, A. G., and R. W. ALLARD. 1965. Population studies in predominantly self-pollinated species. VI. Genetic variability between and within natural populations of wild oats, *Avena fatua* L. from differing habitats in California. *Genetics* 51:49-62.
- JAIN, S. K., and B. C. JOSHI. 1962. Local differentiation in some natural populations of *Justicia simplex*. *Genetics* 47:789-792.
- JAIN, S. K., and D. R. MARSHALL. 1967. Population studies in predominantly self-

- pollinating species. X. Variation in natural populations of *Avena fatua* and *A. barbata*. Amer. Naturalist 101:19-33.
- KEARNEY, T. H., and R. H. PEEBLES. 1951. Arizona flora. Univ. California Press, Berkeley.
- KNOWLES, P. F. 1943. Improving an annual brome grass, *Bromus mollis* L. for range purposes. J. Amer. Soc. Agron. 35:584-594.
- LEWONTIN, R. C. 1965. Selection for colonizing ability. In H. G. BAKER and G. L. STEBBINS (eds.), The genetics of colonizing species. Academic Press, New York.
- MORLEY, F. H. W. 1958. The inheritance and ecological significance of seed dormancy in subterranean clover (*Trifolium subterraneum* L.). Austral. J. Biol. Sci. 11:261-274.
- MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.
- RAVEN, P. H. 1963. A flora of San Clemente Island, California. Aliso 5:289-347.
- SAGAR, G. R., and J. L. HARPER. 1960. Factors affecting the germination and early establishment of Plantains (*Plantago lanceolata*, *P. media* and *P. major*). In J. L. HARPER (ed.), The biology of weeds. Blackwell, Oxford.
- STEBBINS, G. L. 1965. Colonizing species of the native California flora. In H. G. BAKER and G. L. STEBBINS (eds.), The genetics of colonizing species. Academic Press, New York.
- THORNE, R. F. 1967. A flora of Santa Catalina Island, California. Aliso 6:1-77.
- WEIL, J., and R. W. ALLARD. 1965. The mating system and genetic variability in natural populations of *Collinsia heterophylla*. Evolution 18:515-525.

THE POLYPODIUM VULGARE COMPLEX IN THE PACIFIC NORTHWEST

FRANK A. LANG

Department of Biology, Southern Oregon College, Ashland 97520

INTRODUCTION

The *Polypodium vulgare* complex in the Pacific Northwest has been a problem to taxonomists since a number of names have been applied to ill-defined and inadequately understood taxa. In 1961 the author began a critical study of this complex in northwestern North America using modern biosystematic methods in an effort to clarify the taxonomic situation and if possible to elucidate the evolution of the complex (Lang 1965). The basic findings of this paper have recently been briefly summarized by Taylor (1970). A more detailed discussion is presented here to further clarify the taxonomy and evolution of the complex in the Pacific Northwest.

As defined here, northwestern North America comprises the area from Alaska south along the Pacific Coast to central California and east to the Rocky Mountains. Although most of the populations of the complex examined here were from this area, a number of herbarium specimens from elsewhere in western North America were also studied.